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Dispersal Syndromes Can Impact Ecosystem Functioning In Spatially Structured Freshwater Populations

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Word Count: 2450

Abstract

Dispersal can strongly influence ecological and evolutionary dynamics. Besides the direct contribution of dispersal to population dynamics, dispersers often differ in their phenotypic attributes from non-dispersers, which leads to dispersal syndromes. The consequences of such dispersal syndromes have been widely explored at the population and community level, however, to date, ecosystem-level effects remain unclear. Here, we examine whether dispersing and resident individuals of two different aquatic keystone invertebrate species have different contributions to detrital processing, a key function in freshwater ecosystems. Using experimental two-patch systems, we found no difference in leaf consumption rates with dispersal status of the common native species *Gammarus fossarum*. In *Dikerogammarus villosus*, however, a Ponto-Caspian species now expanding throughout Europe, dispersers consumed leaf litter at roughly three times the rate of non-dispersers. Furthermore, this put the contribution of dispersing *D. villosus* to leaf litter processing on par with native *G. fossarum,* after adjusting for differences in organismal size. Given that leaf litter decomposition is a key function in aquatic ecosystems, and the rapid species turnover in freshwater habitats with range expansions of non-native species, this finding suggests that dispersal syndromes may have important consequences for ecosystem functioning.

Introduction

Dispersal, the movement from a natal site to another site or habitat patch with potential consequences for gene flow, is an essential process in ecology and evolution [1,2]. Dispersal connects local populations and allows for colonization of new patches, and thus governs the spatial distribution of biodiversity. Although it is often treated as a stochastic event, dispersal between patches is neither neutral with respect to species [3] nor to individuals within species [4]. Within species, individuals may disperse depending on their own phenotype (dispersal syndrome) [5–7]. Across the animal kingdom, dispersing and non-dispersing individuals have identifiable differences in a broad range of phenotypic characteristics [2,4,8]. These phenotypic differences can have consequences in the newly colonized habitats.

To date, the effects of dispersal syndromes have primarily been considered at the population and community levels. For example, in Glanville fritillary butterflies, polymorphism in an isomerase gene is such that heterozygotes disperse 70% more often than homozygotes, and because this gene is also associated with differences in clutch size, life span, and other traits, this contributes to colonization-extinction dynamics [2]. In western bluebirds, the increased aggressiveness of dispersers has community-level effects because this enables them to out-compete mountain bluebirds in patches they colonize [9].

While such correlations are interesting in the context of population and community dynamics, ecosystems could also be impacted by dispersal syndromes, via resource flux, a measure of ecosystem functioning [10]. In fact, some work has demonstrated that dispersers consume resources differently than non-dispersers; for example, mosquitofish which had dispersed between pools in an experimental stream were four times as efficient at reducing prey abundance after arriving in a new

location as are non-dispersers, though this effect attenuated over time [11]. However, this finding was framed in a behavioral context of behavior, rather than addressing its potential implications for ecosystem-level fluxes. Thus, resource dynamics, and resource consumption in particular, are a potentially unexplored consequence of dispersal syndromes on ecosystems [12].

Detritus consumption by detritivores is a strong determinant of decomposition rate, one of the key fluxes in ecosystems [13,14]. Decomposition of organic matter is especially important in freshwater ecosystems, because it enables terrestrial detritus to subsidize the aquatic food web [15], and shredding of leaf litter by invertebrate detritivores is a key step in the decomposition process [16,17]. Here, we used shredding freshwater detritivores to test whether dispersers differ in their leaf litter consumption rate and thus their contribution to ecosystem function (decomposition). We used one native and one non-native species of amphipod (Crustacea: Amphipoda), a guild of dominant shredding invertebrates in European streams [18]. Amphipod abundance can drive total terrestrial leaf litter shredding [19,20], however these two species are functionally non-equivalent in their shredding activity [21–23] . After an initial experiment where we allowed individuals to disperse in experimental two-patch landscapes, we examined whether dispersers and non-dispersers (henceforth "residents") differed in leaf consumption rates.

Methods

We used one native amphipods species, *Gammarus fossarum* (Koch), and one non-native amphipod species, *Dikerogammarus villosus* (Sowinsky), in our experiments. *Gammarus fossarum* is very common in headwater streams throughout Switzerland and central Europe [24]. We collected adult *G. fossarum* from the

96 Sagentobelbach stream in Dübendorf, Switzerland (47.39° N, 8.59° E) in November
97 2016. In the laboratory, amphipods were placed in holding containers of ~500
98 individuals, gradually brought up to 18 °C, and acclimated to laboratory conditions
99 for 60 hours, during which ad libitum alder (*Alnus glutinosa* (Gaertner)) leaves were
100 available as food. This was repeated in January 2017 with *D. villosus*, a species which
101 originates in the Ponto-Caspian region and has expanded into central Europe in the
102 last two decades [25], with individuals collected from Lake Constance at Kesswil,
103 Switzerland (47.60° N, 9.32° E). For each species, the experiment was conducted in
104 two steps: a dispersal experiment followed by a leaf consumption experiment.
105 Experimental protocols, including length of dispersal phase and length of
106 consumption experiment, were adapted depending on the species' activity levels and
107 consumption rates, based on pilot experiments. *Gammarus fossarum* used in the
108 experiment had a mean dry weight of 3.30 mg (s.d. ±1.33), and *D. villosus* had a mean
109 dry weight of 8.59 mg (s.d. ±2.60).
110
111 *Dispersal experiment*
112 One of the most common methods for examining the causes and consequences
113 of dispersal is to allow organisms to disperse through linked experimental patches in
114 systems ranging from two-patch pairings [26] to larger grids or networks [27,28]. The
115 dispersal experiments were run according to the Dispersal Network (DispNet)
116 distributed experiment protocol, detailed in [26]. Briefly, we set up 40 replicates of a
117 two-patch mesocosm system, with 10 replicates each in a factorial design of resource
118 availability (alder leaves vs. no food) and predator cues (fish kairomones vs. no
119 kairmones). Because we found no effect of the resource or predator cue context on
120 dispersal rates in amphipods [26], we pooled data from the different treatments

121 together for this analysis and only considered the effect of dispersal status (disperser
122 vs. resident) on subsequent leaf consumption. Residuals from the models (described
123 below) confirmed that no additional variation in leaf consumption rates was explained
124 by experimental context/treatment (Figure S2).

125 Each patch was a 3 L (198 x 198 mm) polypropelene box, and each pair of
126 patches (one "origin" and one "target" patch, with their relative positions randomized
127 within each pair) was connected by 30 cm of silicon tubing with 20 mm diameter.
128 Patches were covered with a black lid to reduce light permeability, while the
129 connection tube was left uncovered; this light difference between patches and matrix
130 rendered the connection tube a hostile matrix, since photophobia is an antipredation
131 strategy in amphipods [29]. We also measured movement (gross swimming speed,
132 extracted from videos of the animals using the 'BEMOVI' package [30] in R), and
133 this did not differ significantly between residents and dispersers (Figure S1). Thus, we
134 are confident that relocation from the origin to target patch was not simply due to
135 routine movement in the course of foraging, but indeed represented dispersal.

136 Twenty amphipods were placed in each origin patch and allowed to habituate
137 for 30 minutes. We then opened a clamp that had been used to close the connection
138 and amphipods could disperse for a period of 4 ½ hours (*G. fossarum)* or 7 hours (*D.*
139 *villosus*) before the connection tube was closed again.

140

141 *Consumption experiment*

142 After the dispersal experiment, amphipods were transferred to new single-
143 patch mesocosms (2 L plastic containers with 0.4 m^2 of substrate area) to measure leaf
144 litter consumption. The density of amphipods used in the leaf consumption
145 experiment was standardized between dispersers and residents to account for possible

146 effects of density on leaf consumption rates [31]. Thus, from each two-patch system,
147 all dispersers were moved to one new mesocosm, and an identical number of
148 haphazardly-chosen residents was moved to a separate new mesocosm. Densities
149 remained highly correlated at the replicate block level throughout the experiment (*G.*
150 *fossarum*: r = 0.89, p < 0.001; *D. villosus*, r = 0.53, p = 0.05). Mesocosms were
151 provisioned with 1.5 g (dry weight) of conditioned alder leaves. The leaf consumption
152 experiments were run for 19 (*G. fossarum*) and 12 (*D. villosus*) days, respectively, at
153 which point leaves from the mesocosms were collected and dried for 48 h at 60 ˚C,
154 then weighed to calculate mass loss from the beginning of the experiment. Amphipods
155 were counted every two to three days throughout the experiments to track mortality;
156 overall, survival was 76.3% for *G. fossarum* and 95.4% for *D. villosus.* These
157 mortality estimates were used to calculate an average daily amphipod density for each
158 mesocosm over the length of the experiment. At the end of the experiment, amphipods
159 were sacrificed and dried for 48 h at 60 ˚C. The average daily biomass in a mesocosm
160 (mg m^{-2}) was then calculated as the average daily density (above) multiplied by the
161 average weight of individuals in the mesocosm. Leaf consumption rates were
162 calculated as the dry weight of leaf litter consumed per milligram of amphipod dry
163 weight per day.
164
165 *Analysis*
166 Consumption rates were compared between residents and dispersers of each
167 species separately using linear mixed-effects models with the 'lme4' package, version
168 1.1-18-1 [32], in R version 3.5.0 (R Core Team, Vienna, Austria, 2018). Distributions
169 of consumption rates were positively skewed, so to meet assumptions regarding error
170 structure the *G. fossarum* data were square-root transformed and the *D. villosus* data

were inverse-transformed (response = 1/consumption rate) before analysis. For both species, the response was modeled with dispersal status (disperser vs. resident) as a fixed factor, and replicate block (the two-patch experimental metapopulation from which dispersers and residents originated) as a random intercept. The replicate block accounted for all potential differences associated with the experimental metapopulation of origin and density. After building the mixed-effect models, a conditional R^2 value (accounting for both random and fixed effects) was calculated using the 'MuMIn' package, version 1.42.1 [33]. Differences in consumption rates between dispersers and residents were tested using Tukey HSD tests using the 'multcomp' package, version 1.4-8 [34].

Results

For *G. fossarum*, the estimated difference between square-root transformed daily consumption rates of residents and dispersers was 0.020 (standard error of the estimate = 0.121; model $R^2 = 0.38$) (Table 1). For *D. villosus*, the estimated difference between inverse-transformed daily consumption rates of residents and dispersers was 0.208 (standard error of the estimate = 0.063; model $R^2 = 0.82$), which was significant according to post-hoc testing ($z = 3.31$, $p < 0.001$, Table 1). Dispersing *D. villosus* had similar biomass-adjusted consumption rates to *G. fossarum*, and approximately three times higher than non-dispersing *D. villosus* (Figure 1).

Discussion

We identified a dispersal syndrome with consequences for ecosystem functioning in a non-native but not a native species: *D. villosus* dispersers consumed leaf litter at roughly three times the rate of residents, while there was no difference in

196 leaf consumption rate with dispersal status in *G. fossarum*. To date, most research
197 addressing consumption rates in relation to dispersal status or range fronts has been in
198 a behavioral context, addressing personality and aggression as contributions to
199 predator-prey interactions [11,35,36]. To our knowledge there has been little research
200 into consumption of basal resources as a component of nonrandom dispersal. This is
201 despite the importance of such traits to energy flows through food webs and
202 ecosystems. Furthermore, differences in traits that may depend on resource
203 consumption – such as size, metabolism, and growth rates [2,8] – with dispersal
204 propensity render resource consumption a logical component of a dispersal
205 phenotype, and thus one which could have consequences for energy fluxes through
206 food webs and ecosystems.

207 Our study species are omnivorous aquatic invertebrates, which despite a wide
208 diet breadth contribute the bulk of leaf litter processing in central European headwater
209 streams [19]. Our results show that in *D. villosus*, dispersers make a greater
210 contribution to the detritus-based pathway integrating terrestrial energy into the food
211 web than do residents. This species also has lower overall contributions to leaf litter
212 processing than *G. fossarum* [21–23], but we suggest that both species identity and
213 dispersal status of individuals within a species could jointly determine their
214 contribution to ecosystem function.

215 Predicting these populations' contributions to ecosystem function is important
216 because *D. villosus* has deemed one of the 100 worst invaders in European freshwater
217 ecosystems [38]. Therefore, its dispersal syndrome should be considered in that
218 context. Because the non-native species is undergoing an active range expansion, the
219 signature of either tradeoffs for increased dispersal ability or selection for success in
220 new habitats is likely more prominent than in populations which are in their range

core (such as the *G. fossarum* populations used in our experiment), consistent with spatial selection theory [41]. Identifying whether this is true or whether the dispersal syndrome is consistent across the range of *D. villosus* would require performing experiments with *D. villosus* from its range core in the Ponto-Caspian region. This would also address whether it is appropriate to make interspecific comparisons of this and other phenotypic traits using populations with different recent dispersal/range expansion histories, depending on the research question.

Regardless, how non-native species will affect ecosystem function is a central question in the era of global change and increased connectivity [42]. As the location of suitable habitat shifts and human activity continues to increase organismal dispersal globally, the potential effects of phenotype-dependent dispersal should be considered when attempting to predict impacts on ecosystem function. This may be challenging, because it means that predictions made based on species contributions to ecosystem function in their range core may not be valid at the edges of their range expansions [42]. However, considering prior evidence of how dispersal phenotypes can alter community dynamics, it is crucial to extend this understanding into the realm of ecosystem function.

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Author contributions

EAF conceived the dispersal experiment and all authors together designed the consumption experiment. CJL and EAF ran the experiments. CJL analyzed the data and drafted the manuscript. All authors contributed to revisions, gave final approval for publication, and agreed to be held accountable for the work within the article.

Data accessibility

Data will be made available on Dryad and code will be posted to GitHub upon the manuscript's acceptance; both are available to reviewers as extra supplementary material.

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Competing interests

We have no competing interests.

Ethical statement

No ethics approval was required for this experiment. Work with non-native species was carried out according to the laws of Switzerland.

Figure/table legends

Figure 1. Daily average leaf litter consumption by dispersing and non-dispersing ("resident") amphipods of *G. fossarum* (n = 73 mesocosms) and *D. villosus* (n = 53), adjusted for biomass of the individuals in each experimental replicate. Error bars show standard error of the mean, and gray dots show raw data points from experimental mesocosms. Asterisk shows a significant difference ($p < 0.05$) between consumption rates of dispersers and residents according to a linear mixed effect model.

Table 1. Results from the linear mixed-effects models of biomass-adjusted consumption rates as a function of dispersal status, for *Gammarus fossarum* (n=73 mesocosms) and *Dikerogammarus villosus* (n=53). Estimates and their standard errors are drawn from linear mixed-effects models, and z- and p-values for the effect of dispersal status are from Tukey's HSD tests; variance associated with the random factor of replicate blocks, and its standard deviation, is reported in italics.

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410
411

412 **Tables**

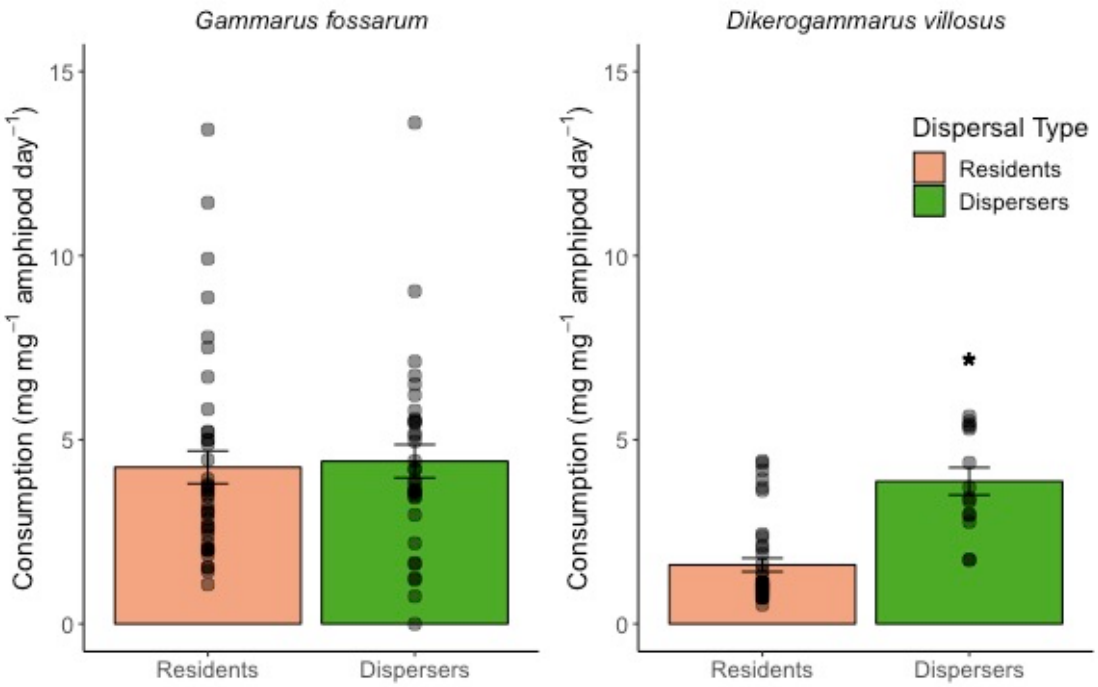
413 **Table 1**

	Coefficient	Std. Error/ Std. Dev.	z	p
G. fossarum **(square-root transformed daily consumption)**				
Intercept (residents)	1.951	0.110		
Dispersers	0.019	0.121	0.163	0.87
Variance due to replicates:	*0.156*	*0.395*		
D. villosus **(inverse-transformed daily consumption**				
Intercept (residents)	0.666	0.080		
Dispersers	0.209	0.063	3.311	< 0.001
Variance due to replicates:	*0.125*	*0.354*		

414

415 **Figures**

416



417

418 **Figure 1.**

Appendix

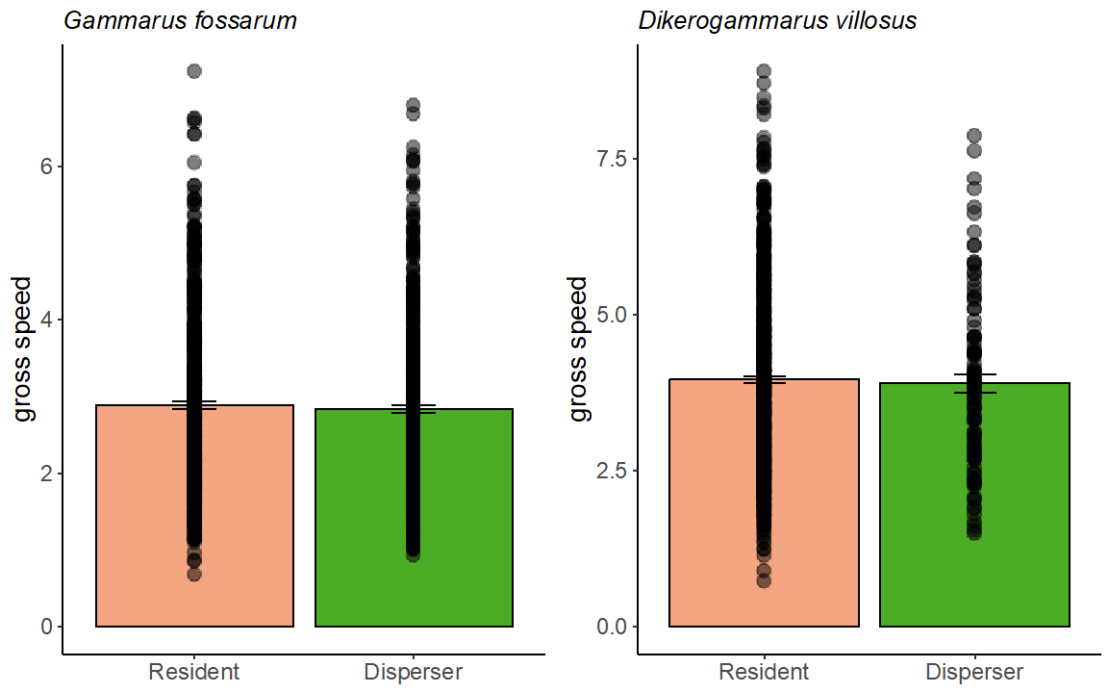
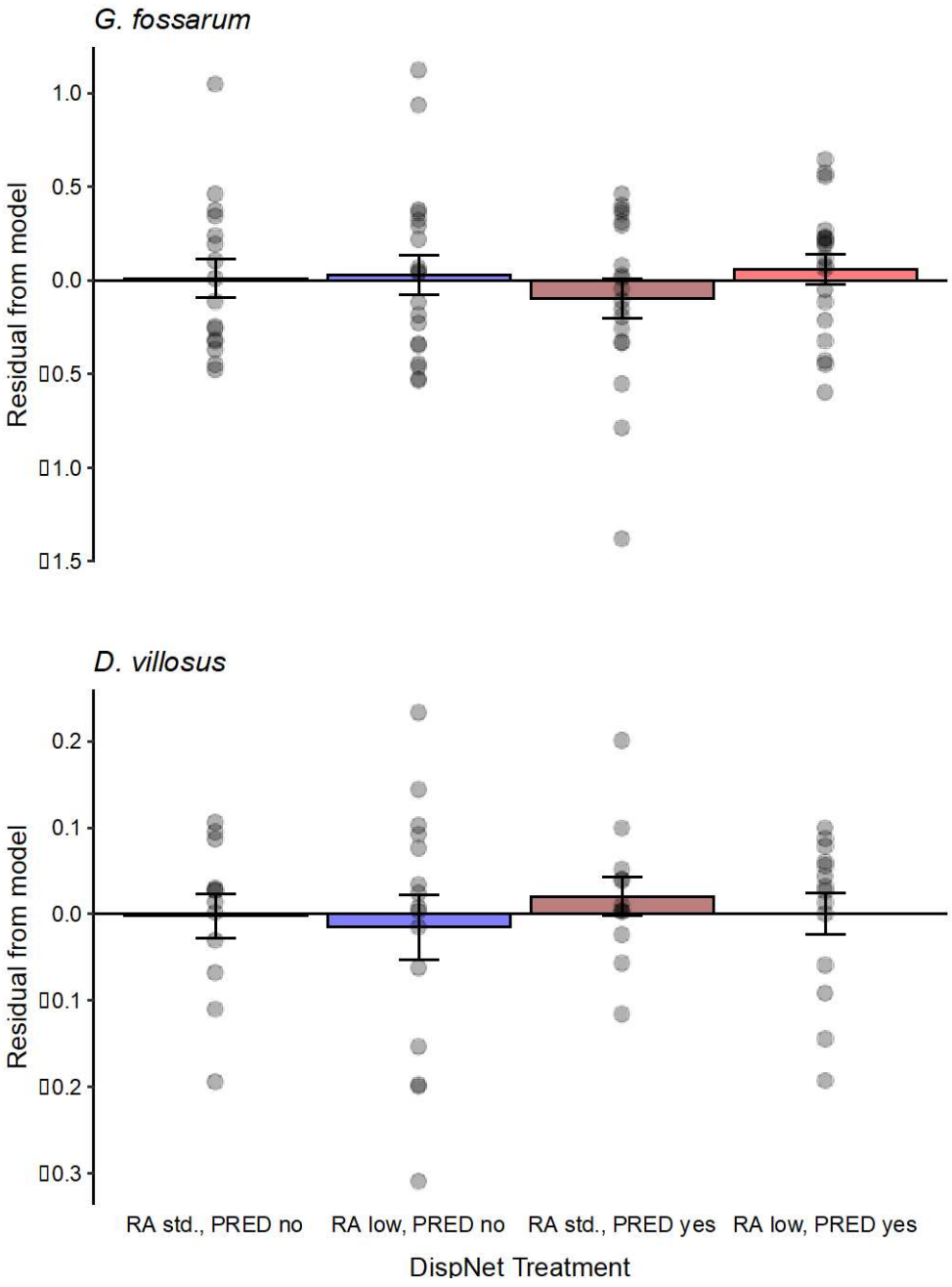


Figure S1. Gross swimming speed of residents and dispers, from video analysis using the 'BEMOVI' package in R. Before being placed into the consumption mesocosms, residents and dispersers were (separately) placed into an experimental arena and and allowed to move freely for three minutes. Each time an amphipod moved it was detected it was given an object identifier and the movement was described; gray dots in the figure represent each movement, and error bars show the standard error of speed for residents and dispersers. There were no significant differences in swimming speed between residents and dispersers based on simple linear models in either *G. fossarum* ($F_{1,1109} = 0.57$, $p = 0.44$) or *D. villosus* ($F_{1,824} = 0.17$, $p = 0.68$).



433

434 **Figure S2**. Model residuals from the mixed-effect models (transformed consumption
435 rate ~ dispersal status + (1|replicate block)) plotted against treatments from the
436 dispersal experiment: RA = resource availability (standard or low), PRED = predator
437 cues (no or yes). Linear models of residuals as a response of dispersal experiment
438 treatment showed no significant effects (*G. fossarum*: $F_{3,69} = 0.49$, $p = 0.69$; *D.*
439 *villosus*: $F_{3,49} = 0.25$, $p = 0.86$). Error bars show standard error of the mean, and gray
440 points show residuals from individual experimental replicates.